



# Alien plants in Central European river ports

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#### **Abstract**

River ports represent a special type of urbanized area. They are considered to be an important driver of biological invasion and biotic homogenization on a global scale, but it remains unclear how and to what degree they serve as a pool of alien species. Data for 54 river ports (16 German, 20 Czech, 7 Hungarian, 3 Slovak, and 8 Austrian ports) on two important Central European waterways (the Elbe-Vltava and Danube waterways) were collected over 40 years. In total, 1056 plant species were found. Of these, 433 were alien, representing 41% of the total number of species found in all the studied Elbe, Vltava, and Danube ports. During comparison of floristic data from literary sources significant differences in the percentage of alien species in ports (50%) and cities (38%) were found. The number of alien species was closely related to port size, but the proportion of alien species expressed as a percentage of the total number of species did not depend significantly on port area. The proportion of alien species in both studied waterways decreased with distance from the sea and was highest in the Hungarian ports and lowest in the Czech Republic, Austria and Bavaria. Lower levels of shipping towards inland regions due to decreased river flow are likely the reason for this trend. The dissimilarity in the species composition of alien and native flora between individual river ports increased with increasing inter-port distance. Neophytes presented a stronger distance decay pattern than did either native species or archaeophytes of the Danube inland ports, potentially due to the different cargoes of individual ports, which may affect the introduction of different neophytes from different geographic areas. The results show that river ports in Central Europe should be regarded as a type of industrial area and deserve full attention with regard to the distribution and spread of alien plants.

#### Keywords

Alien plants, Central Europe, river ports, waterway

#### Introduction

Many studies have demonstrated that cities are hotspots of alien plants (e.g. Pyšek 1998; Sukopp 2002; Wittig 2002; Clemants and Moore 2003; Zerbe et al. 2004; Ricotta et al. 2009; Zhao et al. 2010; Lososová et al. 2012; Aronson et al. 2014). A main reason for this is that urbanized areas provide suitable environments for alien species, with superior conditions for their development compared to those available in rural areas (e.g. Kühn and Klotz 2006; von der Lippe and Kowarik 2008). This suitability of urbanized areas especially applies to neophytes (taxa introduced after AD 1500), whose presence among urban flora over the last 100 years or longer has increased significantly (Godefroid 2001; Chocholoušková and Pyšek 2003; DeCandido 2004; Knapp et al. 2010).

The development of international trade and transport and the related global dispersal of invasive alien species have had significant impacts on the spread of alien species among urbanized areas (Levine and D'Antonio 2003; Dehnen-Schmutz et al. 2007; Westphal et al. 2008). Traffic junctions and transshipment points of goods have had an important role, as they represent the sources of occurrence and spread of invasive plants (Jehlík and Hejný 1974; Forcella and Harvey 1988; Kornaś 1990; Jehlík et al. 1998; Song and Prots 1998). For this reason, urban-industrial areas are regarded as the main drivers of biological invasions (Wittig 2010).

Within urban-industrial environments, port areas represent introduction hubs for alien species whose seeds are spread with shipping (Wittig 2004; Adhikari et al. 2015). Some cargoes provide excellent means for the transportation of seeds or entire plants (e.g., food and animal feed, minerals, coal, solid ballast). Port areas have been extensively explored with respect to marine invasive species (Molnar et al. 2008). Attention has also been paid to terrestrial plant species, which can also benefit from marine/ freshwater transportation routes (Anastasiu et al. 2011; Jehlík 2013). The presence of alien plants among the flora of seaports in the north of Europe has been reported for Poland (Čwikliński 1970; Misiewicz 1985), Norway (Ouren 1978, 1980, 1983, 1987), Germany (Jehlík 1981, 1989, 1994a), the Netherlands (Jehlík and Dostálek 2015), and Ireland (Reynolds 1990). Information on the occurrence of alien plants in the Black Sea ports in the territory of Ukraine is reported by Petryk (1993), and the role of ports in the spread of alien plants along the Romanian Black Sea was analysed by Anastasiu et al. (2011). In addition, the relationship between the occurrence of alien plants and urban habitat type in the port of Trieste on the Adriatic coast was explored in detail by Tordoni et al. (2017).

Marine ports are typically connected to inland waterway networks; the connections facilitate the inland spread of alien plants, especially through river ports. Port-Juvénal, the port of Montpellier (France) on the river Lez, is a classic case for the role of inland ports for the introduction of alien plants. Thellung (1912) reported the arrival of many alien plant species, most of which have been introduced into the area through imports of wool (see details: Kowarik and Pyšek 2012). Most data on the occurrence of alien

plants in the river ports of central Europe come from Germany (Ludwig 1957; Stricker 1962; Schäfer 1965; Runge 1965; Stieglitz 1980, 1981; Klotz 1984; Brandes 1989; Jehlík 1994b; Brandes and Sander 1995; Lotz 1998; Düring 2004). Additional data come from Poland (Szotkowski 1978), Belgium (Verloove 1992), Switzerland (Baumgartner 1973, 1985), the Czech Republic and Slovakia (Eliáš 1985; Jehlík 1985, 2008; Jehlík et al. 2005). River ports typically occur in industrial areas that are part of the urban matrix and whose alien flora has not yet been systematically studied. Using data from a 40-year study of flora and vegetation in 54 river ports of Central Europe (Jehlík 2013), this paper presents detailed information on alien plants that occur in this specific type of industrialized area.

The following questions are addressed:

1. What is the proportion of alien species in the flora of Central European river ports, and does it differ from the proportions in other urbanized areas? 2. To what extent does the size of a port influence the abundance of alien plants? 3. Does the amount of alien species differ among various river systems (regions)? 4. Is the floristic composition in river ports related to the distance of the port from the sea or the distance between ports?

### Methods

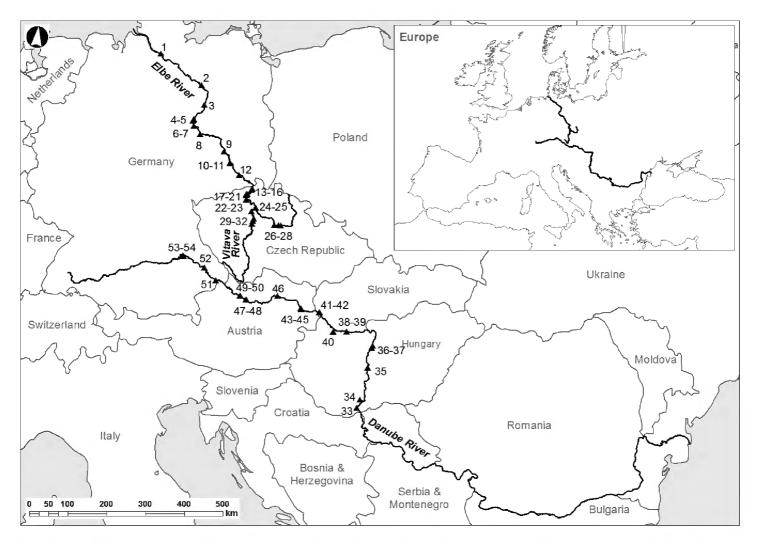
The data used for the analysis were collected over the course of long-term floristic research activities conducted during 1968–2009 in 54 river ports in five countries in Central Europe (Czech Republic, Germany, Austria, Slovakia, Hungary) by the first author (Jehlík 2013). The ports were studied in two different river systems belonging to the most important waterways of Central Europe. A total of 32 ports were located in the Elbe-Vltava waterway between 50° and 53° N, and a total of 22 ports were located on the Danube River between 45° and 49° N (Table 1, Fig. 1).

The ports were visited several times during various periods of the growing season to maximize the possibility of sampling the full species composition (see Appendix 2). After 41 years, lists of taxa from all 54 locations were compiled. To record the abundances of plant taxa, a five-degree scale (sporadic, rare, scattered, abundant, highly abundant) derived from the Braun-Blanquet approach (Braun-Blanquet 1964; Westhoff and van der Maarel 1978) was used. To calculate the floristic dissimilarity between ports and the difference in individual species representation between waterways, the degrees of the scale were transformed into numeric values: sporadic (one or two individuals) = 1, rare = 2, scattered = 3, abundant = 5, and highly abundant = 7. To statistically evaluate the effect of port size on species richness for all focal species groups, the area of each port locality was measured using Google Earth Pro 7.1. To compare the presence of alien species between the investigated river ports and other urbanized areas, previously published floristic data for 29 cities were compiled and analyzed (Pyšek 1998; Table 2), and the data were tested for differences using the Mann-Whitney U test.

**Table 1.** Native and alien plant species in the flora of 54 Central European river ports, including the total number and proportion of species of different categories, identified in each port.

| River port (country)  | Number of species |        |                 |                    |                | Proportion of species [%] |                 |                    |                |
|---|-------------------|--------|-----------------|--------------------|----------------|---------------------------|-----------------|--------------------|----------------|
|   | Total             | Native | Total<br>aliens | Archae-<br>ophytes | Neo-<br>phytes | Native                    | Total<br>aliens | Archae-<br>ophytes | Neo-<br>phytes |
| Elbe and Vltava Rivers  |                   |        |                 |                    |                |                           |                 |                    |                |
| 1. Hamburg (Germany)  | 360               | 153    | 207             | 98                 | 69             | 48                        | 52              | 31                 | 21             |
| 2. Wittenberge (Germany)  | 197               | 79     | 118             | 75                 | 37             | 41                        | 59              | 39                 | 20             |
| 3. Tangermünde (Germany)  | 170               | 76     | 94              | 60                 | 33             | 45                        | 55              | 35                 | 20             |
| 4. Magdeburg-Rothensee (Germany)                                | 133               | 48     | 85              | 52                 | 32             | 36                        | 64              | 40                 | 24             |
| 5. Magdebur, Industriehafen (Germany)                           | 283               | 120    | 163             | 98                 | 58             | 43                        | 57              | 36                 | 21             |
| 6. Magdeburg, Handelshafen (Germany)                            | 353               | 150    | 203             | 117                | 74             | 44                        | 56              | 34                 | 22             |
| 7. Schönebeck-Frohse  | 229               | 100    | 129             | 90                 | 37             | 44                        | 56              | 40                 | 16             |
| 8. Aken, Handelshafen (Germany)                                 | 250               | 123    | 127             | 93                 | 34             | 49                        | 51              | 37                 | 14             |
| 9. Torgau (Germany)   | 245               | 121    | 124             | 78                 | 36             | 51                        | 49              | 33                 | 16             |
| 10. Riesa-Gröba, Industriehafen (Germany)                       | 354               | 174    | 180             | 111                | 62             | 50                        | 50              | 32                 | 18             |
| 11. Riesa, transshipment point at mill houses (Germany)         | 282               | 133    | 149             | 87                 | 50             | 49                        | 51              | 32                 | 19             |
| 12. Dresden, Albertshafen (Germany)                             | 333               | 158    | 175             | 103                | 56             | 50                        | 50              | 32                 | 18             |
| 13. Děčín-Loubí (Czech Republic)                                | 336               | 147    | 189             | 92                 | 59             | 49                        | 51              | 31                 | 20             |
| 14. Děčín-Staré Loubí (Czech Republic)                          | 279               | 161    | 118             | 73                 | 39             | 59                        | 41              | 27                 | 14             |
| 15. Děčín-Staré Město (Czech Republic)                          | 153               | 82     | 71              | 46                 | 25             | 54                        | 46              | 30                 | 16             |
| 16. Děčín-Rozbělesy (Czech Republic)                            | 267               | 184    | 83              | 54                 | 29             | 69                        | 31              | 20                 | 11             |
| 17. Ústí nad Labem-Krásné Březno (Czech Republic)               | 323               | 142    | 181             | 100                | 55             | 48                        | 52              | 34                 | 18             |
| 18. Ústí nad Labem, Central Port (Czech Republic)               | 251               | 125    | 126             | 81                 | 43             | 50                        | 50              | 33                 | 17             |
| 19. Ústí nad Labem, Western Port (Czech Republic)               | 327               | 140    | 187             | 101                | 54             | 47                        | 53              | 34                 | 19             |
| 20. Ústí nad Labem, Větruše (Czech Republic)                    | 227               | 121    | 106             | 60                 | 38             | 55                        | 45              | 28                 | 17             |
| 21. Ústí nad Labem-Vaňov (Czech Republic)                       | 234               | 127    | 107             | 71                 | 35             | 55                        | 45              | 30                 | 15             |
| 22. Lovosice, Canal Port (Czech Republic)                       | 232               | 85     | 147             | 85                 | 49             | 39                        | 61              | 39                 | 22             |
| 23. Lovosice-Prosmyky (Czech Republic)                          | 246               | 110    | 136             | 93                 | 39             | 45                        | 55              | 39                 | 16             |
| 24. Mělník-Pšovka (Czech Republic)                              | 333               | 148    | 185             | 110                | 57             | 47                        | 53              | 35                 | 18             |
| 25. Mělník, Transshipment Point (Czech Republic)                | 266               | 144    | 122             | 79                 | 43             | 54                        | 46              | 30                 | 16             |
| 26. Kolín, Transshipment Point (Czech Republic)                 | 225               | 101    | 124             | 84                 | 39             | 45                        | 55              | 38                 | 17             |
| 27. Týnec nad Labem, Ro-Ro-Transshipment Point (Czech Republic) | 216               | 138    | 78              | 52                 | 26             | 64                        | 36              | 24                 | 12             |
| 28. Chvaletice (Czech Republic)                                 | 178               | 125    | 53              | 34                 | 19             | 70                        | 30              | 19                 | 11             |
| 29. Miřejovice Ro-Ro-Transshipment Point (Czech Republic)       | 236               | 138    | 98              | 66                 | 30             | 59                        | 41              | 28                 | 13             |
| 30. Praha-Holešovice (Czech Republic)                           | 388               | 187    | 201             | 119                | 69             | 50                        | 50              | 32                 | 18             |
| 31. Praha-Smíchov (Czech Republic)                              | 216               | 93     | 123             | 80                 | 37             | 44                        | 56              | 38                 | 18             |
| 32. Praha-Radotín (Czech Republic)                              | 162               | 68     | 94              | 65                 | 26             | 43                        | 57              | 41                 | 16             |
| Danube river  |                   |        |                 |                    |                |                           |                 |                    |                |
| 33. Mohács, Transshipment Point (Hungary)                       | 183               | 79     | 104             | 65                 | 36             | 44                        | 56              | 36                 | 20             |
| 34. Baja (Hungary)  | 305               | 134    | 171             | 106                | 59             | 45                        | 55              | 35                 | 20             |
| 35. Dunaújváros (Hungary)                                       | 250               | 105    | 145             | 95                 | 45             | 43                        | 57              | 39                 | 18             |
| 36. Budapest-Csepel (Hungary)                                   | 280               | 93     | 187             | 109                | 64             | 35                        | 65              | 41                 | 24             |
| 37. Budapest-Ferencváros (Hungary)                              | 205               | 78     | 127             | 83                 | 38             | 39                        | 61              | 42                 | 19             |
| 38. Györ, Transshipment Point (Hungary)                         | 249               | 108    | 141             | 87                 | 46             | 45                        | 55              | 36                 | 19             |
| 39. Györ, Commercial Port "Iparcsatorna" (Hungary)              | 166               | 61     | 105             | 69                 | 34             | 37                        | 63              | 42                 | 21             |
| 40. Komárno (Slovakia)  | 338               | 135    | 203             | 123                | 70             | 41                        | 59              | 38                 | 21             |
| 41. Bratislava-Pálenisko (Slovakia)                             | 322               | 150    | 172             | 106                | 57             | 48                        | 52              | 34                 | 18             |
| 42. Bratislava-Nivy (Slovakia)                                  | 411               | 182    | 229             | 133                | 78             | 46                        | 54              | 34                 | 20             |
| 43. Wien-Lobau (Austria)  |                   | 167    |                 |                    |                |                           |                 |                    |                |
| 43. wich-lobau (Austria)  | 293               | 10/    | 126             | 85                 | 37             | 58                        | 42              | 29                 | 13             |

| River port (country)                             | Number of species |        |                 |                    | Proportion of species [%] |        |                 |                    |                |
|--|-------------------|--------|-----------------|--------------------|---------------------------|--------|-----------------|--------------------|----------------|
|  | Total             | Native | Total<br>aliens | Archae-<br>ophytes | Neo-<br>phytes            | Native | Total<br>aliens | Archae-<br>ophytes | Neo-<br>phytes |
| 44. Wien-Albern (Austria)                        | 295               | 128    | 167             | 117                | 46                        | 44     | 56              | 40                 | 16             |
| 45. Wien-Freudenau (Austria)                     | 307               | 138    | 169             | 113                | 54                        | 45     | 55              | 37                 | 18             |
| 46. Krems an der Donau (Austria)                 | 294               | 140    | 154             | 105                | 42                        | 49     | 51              | 36                 | 15             |
| 47. Ennsdorf, Hafenbecken Ost, Silos (Austria)   | 276               | 150    | 126             | 76                 | 43                        | 56     | 44              | 28                 | 16             |
| 48. Enns (Austria)                               | 389               | 231    | 158             | 92                 | 52                        | 62     | 38              | 24                 | 14             |
| 49. Linz, Tankhafen (Austria)                    | 229               | 138    | 91              | 66                 | 25                        | 60     | 40              | 29                 | 11             |
| 50. Linz, Handelshafen /Stadthafen (Austria)     | 324               | 169    | 155             | 99                 | 51                        | 53     | 47              | 31                 | 16             |
| 51. Passau-Racklau (Germany)                     | 252               | 135    | 117             | 80                 | 35                        | 54     | 46              | 32                 | 14             |
| 52. Deggendorf (Germany)                         | 202               | 124    | 78              | 56                 | 22                        | 61     | 39              | 28                 | 11             |
| 53. Regensburg, Osthafen (Germany)               | 308               | 164    | 144             | 95                 | 43                        | 54     | 46              | 32                 | 14             |
| 54. Regensburg Westhafen/Luitpoldhafen (Germany) | 296               | 146    | 150             | 96                 | 47                        | 51     | 49              | 33                 | 16             |



**Figure 1.** Map of Central European river ports whose floras were used in the analysis. Detailed information about individual ports is presented in Table 1.

The species were classified according to their immigration status (for details, see Pyšek 1995; Richardson et al. 2000; Pyšek et al. 2002; Blackburn et al. 2011): (i) A native (indigenous) species is a species that evolves in the area or arrives there either before the beginning of the Neolithic period or after the beginning of that period but in a way entirely independent of human activity (Webb 1985); (ii) An alien (introduced, exotic, adventive) species is a species that reaches the area as a consequence of man or the presence of domestic animals. Two main categories of alien species were used in the

Proportion of archaeophytes

Proportion of neophytes

|                         | Ports                   | Cities        |
|-------------------------|-------------------------|---------------|
| Number of cases         | 54                      | 29            |
| Total number of species | $260 \pm 59$            | 747 ± 321     |
| Number of aliens        | $131 \pm 34$            | $294 \pm 160$ |
| Number of archaeophytes | $86 \pm 22$             | 96 ± 33       |
| Number of neophytes     | 45 ± 14                 | 198 ± 135     |
| Proportion of aliens    | 50 (30–65) <sup>a</sup> | 38 (20–56) b  |

33 (19-42) a

17 (11–24) b

13 (8–19) b

25 (11-42) a

**Table 2.** Presence of alien species in ports and cities. Means ± SD or range in parenthesis are given. Statistically significant differences of proportions between ports and cities are indicated by different letters (Mann-Whitney U test).

analysis: (i) archaeophytes (introduced to Central Europe before the year 1500, mostly from the Mediterranean region) and (ii) neophytes (introduced after the year 1500). Casuals, which do not form self-replacing populations, were not considered. The classification of alien species followed the national lists of alien plants and specialized databases (Klotz et al. 2002; Pyšek et al. 2002, 2012; DAISIE 2009).

Floristic pairwise dissimilarity was calculated as the percentage dissimilarity (Gaugh 1982) separately for the ports of the Elbe-Vltava waterway and Danube waterway. The significance of the correlation coefficients of the relationship between geographical distance and floristic dissimilarity of the ports was tested by Mantel test. The significance of differences between regression coefficients was assessed by the self-made algorithm according to Diem (1960: 178–180). The relationship between species richness and port size was examined by regression analysis (non-linear power function was used). Differences in the abundance of alien species between waterways were tested using Mann-Whitney U test. The program STATISTICA 9.0 (StatSoft Inc. 2009) was used for the analyses. A Principal Components Analysis (PCA) (program CANOCO; ter Braak and Šmilauer 2012) was performed to examine the relationship between the proportion of the number of alien and native species and both waterways and individual regions.

#### Results

### Richness of alien species in the river ports

Overall, 1056 plant taxa were found in the 54 studied river ports. Of these, 193 species were present only in the Elbe-Vltava waterway, and 249 species occurred only in the Danube waterway. The remaining 614 species were found in both river systems.

Of the total number of species, 433 were alien, representing almost half (41%) of the total number of species in the studied Elbe, Vltava, and Danube ports. Sixty-five alien species were found only in the ports of the Elbe-Vltava waterway (i.e., 15% of the total number of alien species), and 72 were found only in the Danube ports (i.e., 17% of the total number of alien species).

On average, there were 125 alien species per river port in the Elbe-Vltava waterway and 140 alien species per port in the Danube waterway. The number of alien species in individual ports ranged between 53 and 191 in the Elbe-Vltava waterway and between 78 and 211 alien species in the Danube waterway (Table 1). The total proportion of alien species in the Elbe-Vltava waterway averaged 50%, with archaeophytes contributing 33% and neophytes contributing 17%. The total proportion of alien species in the Danube waterway averaged 51%, with archaeophytes contributing 34% and neophytes contributing 17%.

Regarding species-area relationships, there were more species in larger ports than in smaller ones [SPECIES NUMBER = 149 \* (PORT AREA m<sup>2</sup>)<sup>0.046</sup>; R<sup>2</sup> = 0.171; p = 0.005]. This was also true when considering alien species alone [ALIEN SPECIES NUMBER = 69 \* (PORT AREA m<sup>2</sup>)<sup>0.053</sup>; R<sup>2</sup> = 0.173; p = 0.005]. However, the proportion of alien species expressed as a percentage of the total number of species did not vary significantly with port area (R<sup>2</sup> = 0.0175; non-significant).

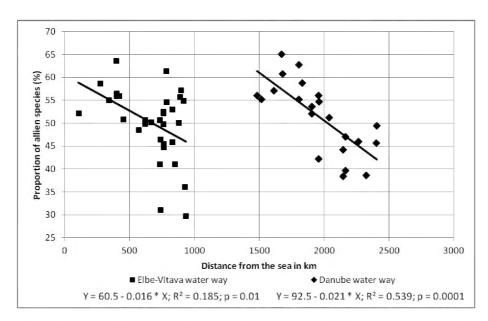
## Role of a distance to the sea and other ports

The relationship between the number of alien species in a port and the distance of the port from the sea is presented in Figure 2. The proportion of alien species in both studied waterways decreased with increasing distance from the sea. This pattern was also observed when considering the archaeophytes and neophytes separately.

The floristic dissimilarity values for the 496 unique pairwise combinations of flora in 32 river ports of the Elbe-Vltava waterway and for the 231 combinations of flora in 22 Danube inland ports presented divergent decay patterns for the native species, archaeophytes, and neophytes (Fig. 3). In general, the similarity in species composition between individual river ports of both waterways decreased with inter-port distance in the case of both alien and native flora. All correlations were significant (Mantel test, p = 0.008-0.0001). However, in the ports of Elbe-Vltava waterway native and allien species dissimilarity expressed similar slope (i.e. the regression lines are parallel), while in the ports of Danube waterway archaeophytes and native species presented the weakest pattern of distance decay, whereas neophytes presented the strongest pattern. The difference between the regression coefficients was significant (p = 0.016 and 0.015 for the comparison of archeophytes × neophytes and native species × neophytes, respectively).

## Comparison with urban floras

The data presented in Table 2 show that the percentage of the total number of alien species reported from the ports (50%) is significantly higher than that observed in the cities (38%). However, significant differences in the proportions of archaeophytes and neophytes were found between ports and cities. The percentage of archaeophytes in ports (33%) was significantly higher than that in cities (13%), whereas the percentage of neophytes in ports (17%) was significantly lower than that in cities (25%).



**Figure 2.** Relationship between the proportion of the number of alien species in studied river ports and the distance from the sea.

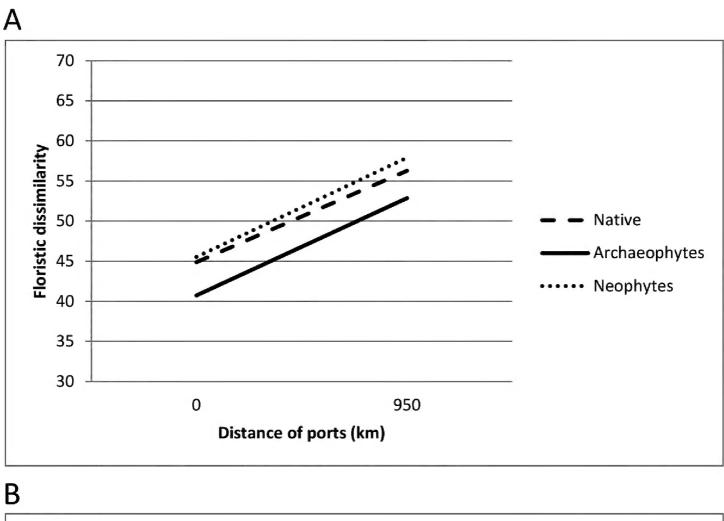
## Comparisons between the Elbe-Vltava and Danube waterways

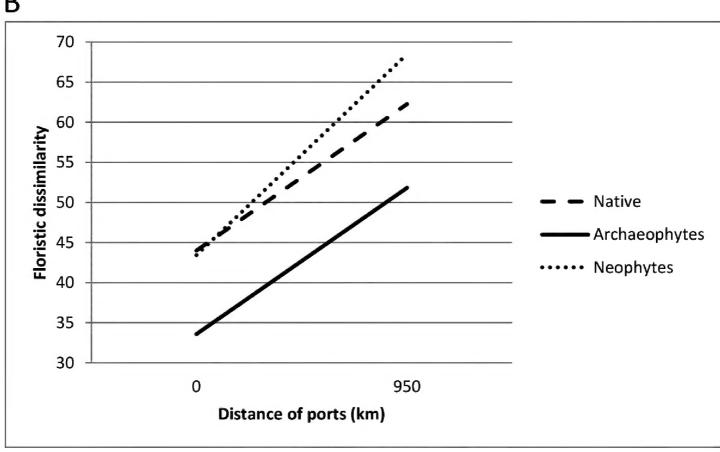
Results of Principal Component Analysis (PCA) shown in Figure 4 do not indicate remarkable difference in the proportion of alien species between the Elbe-Vltava and Danube waterways. The ratio of alien and native species decreases with the distance from the sea. The highest proportion of alien species was found in Hungarian ports (especially archaeophytes), followed by the ports in the northern parts of Germany and Slovakia with higher proportion of neophytes. The lowest proportions of alien species were found in the upper parts of the rivers; specifically, in the Elbe and Vltava ports in the Czech Republic and in the Danube ports in Austria and Bavaria.

Most alien species (only species that occurred in at least five ports were tested) were similarly distributed in both waterways. However, some species occurred more frequently in the Elbe-Vltava waterway, whereas other species were more often observed in the Danube waterway. The number of alien species that were significantly more abundant in the Danube ports than in the Elbe-Vltava ports was higher than the number of alien species that were significantly more abundant in Elbe-Vltava ports (see Appendix 1).

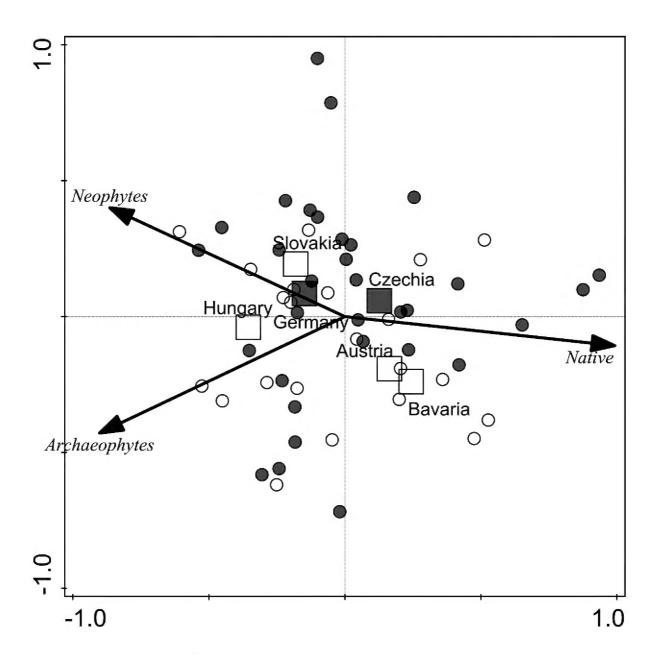
#### Discussion and conclusions

The results of this study demonstrate that river ports contain high proportions of alien plant species. The abundance of alien species increases with port area. This pattern exists because small ports do not have as many large and diverse sites that are suitable for vegetation cover to develop as large ports. In addition, smaller ports have less shipping activity, which contributes less to the intensive spread of alien plants. The proportion of alien species in both studied waterways decreased in relation to port distance from the sea. Consistent with this finding, a higher proportion of alien species was observed





**Figure 3.** Relationship between the floristic dissimilarity of native and alien floras of studied river ports and the geographical distance of ports of the individual waterways. A. Elbe-Vltava waterway. Regression lines for native species (Y = 45 + 0.012X; R<sup>2</sup> = 0.111; p = 0.0025) and two categories of alien species: archaeophytes (Y = 41 + 0.013X; R<sup>2</sup> = 0.081; p = 0.007) and neophytes (Y = 46 + 0.013X; R<sup>2</sup> = 0.082; p = 0.0082). B. Danube waterway. Regression lines for native species (Y = 44 + 0.019X; R<sup>2</sup> = 0.292; p = 0.0001) and two categories of alien species: archaeophytes (Y = 34 + 0.019X; R<sup>2</sup> = 0.279; p = 0.0001) and neophytes (Y = 43 + 0.026X; R<sup>2</sup> = 0.420; p = 0.0001).



**Figure 4.** Ordination diagram (PCA) of proportion of the number of alien and native species in the river ports. The first two axes explain 99% of the total variation, individual regions account for 33% of variation. Circles = ports, squares = countries; closed symbols = ports and regions on the Elbe-Vltava waterway; open symbols = ports and regions on the Danube waterway.

in countries whose river ports are more closely connected to the sea. Lower levels of shipping towards inland regions due to decreased river flow are likely the reason for this trend. The importance of traffic in the spread and subsequent naturalization of alien plants in urbanized areas has been documented, e.g. by von der Lippe and Kowarik (2007), Hulme (2009), and Lembrechts et al. (2015).

The similarity in the species composition of alien flora between individual river ports decreased with distance in the same way as the similarity in native flora. In case of the Elbe-Vltava waterway, the slope of the regression lines is the same and the correlation dissimilarity/distance of all three groups of species was weaker, whereas in the case of the Danube waterway, the neophyte dissimilarity increases with the distances of ports much faster than the dissimilarity of the archaeophytes and native species. In addition, in the case of the Danube waterway, the correlation dissimilarity/distance of all three groups of species is closer. The differences in the correlation power of groups of species between both waterways might be due to the different abiotic factors and

historical land use (see Deutschewitz et al. 2003). The stronger distance decay patterns observed in neophytes of the Danube waterway supports the findings of La Sorte et al. (2008), showing that archaeophytes present the weakest distance decay patterns. In contrast, neophytes presented the strongest distance decay patterns, whereas native species presented intermediate decay patterns. La Sorte et al. (2008) attributed this trend to the fact that the European archaeophytes that exist today represent a set of species that developed successful associations with anthropogenic activities over several millennia. In the case of ports, this scenario implies that archaeophytes have had more time than other alien species to disperse among anthropogenic harbor sites, which are often similar. No significant differences in species richness were found between the two river systems. In addition, the proportion of alien species did not differ between the climatically warmer region (the Danube waterway) and the colder northwestern region (the Elbe-Vltava waterway) of southeastern Central Europe. The data differ in this regard from those of Lososová et al. (2012) and Schmidt et al. (2014), who, after analyzing floristic data from Central European cities, concluded that the proportion of native species decreased with increasing mean annual precipitation. The number of alien species with a significantly stronger relationship to one waterway was higher for the ports on the Danube River than for those on the Vltava and Elbe Rivers, which indicates a favorable influence of warmer climate on the success of alien species in urbanized areas (e.g. Pyšek 1998; Lososová et al. 2012). This influence can also be explained by the higher presence of species from southeastern Europe. A number of these thermophilous species have found suitable habitats in the ports of Central Europe. To a great extent, the differences in species richness and presence of alien species among the individual ports are likely dependent on the size, type, and treatment of port localities.

Our results also indicate that the proportion of the total number of alien species is significantly higher than the proportions reported from urbanized areas in larger European cities and summarized by Pyšek (1998). However, the proportion of archaeophytes in ports was significantly higher than that in cities, while the proportion of neophytes in ports was significantly lower than that in cities. The higher proportion of archaeophytes, which represent a heterogeneous group in terms of the degrees of adaptation to local conditions (see Pyšek and Jarošík 2005), is likely supported by the presence of a high number of diverse habitats with different levels of disturbance in ports. The lower proportion of neophytes reflects the smaller area of port habitat that is suitable for their development (see Celesti-Grapow et al. 2006). These observations demonstrate that a high number of alien species are present in a relatively small area in the river ports.

The results of the flora composition analysis of the studied ports showed that in Central Europe, the river ports belong to the species-rich urbanized areas, with a high presence of alien species. Our results support the findings of Ricotta et al. (2010), indicating that aliens tend to have different environmental requirements than natives. Ports must be regarded as a unique type of species-rich industrial area, deserving full attention with regard to the control of invasive alien plants as well as nature conservation (Jehlík et al. 2016). When planning port development, both of these aspects should be considered.

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# Appendix I

# Overview of the distribution of the alien plants in the inland ports of the river Elbe-Vltava and the river Danube

Statistical significance was tested using 5-degree abundance scale. Only species that occurred in at least 5 ports were tested. For the species statistically differently distributed between the waterways, frequency (%) of the occurrence in the ports of Elbe-Vltava / Danube waterway follows the species name.

The species (taxa) significantly more abundant in the Elbe-Vltava waterway ports:

Aethusa cynapium 22/0
Ambrosia trifida 22/0
Arctium tomentosum 44/14
Asparagus officinalis 44/9
Atriplex oblongifolia 72/45
Atriplex sagittata 91/36
Bidens frondosa 100/77
Carduus crispus 75/32
Chelidonium majus 88/59
Chenopodium pedunculare 84/55
Chenopodium striatiforme 50/14

Chenopodium suecicum 84/41 Datura tatula 31/5

Erysimum cheiranthoides 94/23
Fumaria officinalis 38/14
Galinsoga ciliata 81/45
Galinsoga parviflora 94/73
Hordeum jubatum 25/0
Hyoscyamus niger 47/14

Impatiens glandulifera 44/9
Iva xanthiifolia 53/23
Lamium album 94/14
Leonurus intermedius 25/0
Lepidium latifolium 19/0
Linum usitatissimum 47/14

Lycopsis arvensis subsp. arvensis 31/0

Malva pusilla 19/0
Papaver dubium 50/9
Papaver somniferum 44/14
Rumex thyrsiflorus 88/45

Setaria viridis subsp. pycnocoma 47/18

Sisymbrium loeselii 100/82 Sisymbrium officinale 81/55 Tanacetum vulgare 97/82 Thlaspi arvense 91/45

Tripleurospermum inodorum 100/100

Xanthium albinum 72/9

The species (taxa) significantly more abundant in the Danube waterway ports:

Amaranthus albus 44/82 Amaranthus blitoides 9/36 Amaranthus powellii 88/95 Ambrosia artemisiifolia 53/86 Amorpha fruticosa 0/23 Anagallis arvensis 31/64

Anthemis austriaca 9/36

Anthemis ruthenica 3/23 Anthriscus caucalis 19/59 Anthriscus cerefolium subsp. trichosperma 0/36

Atriplex tatarica 19/59

Bromus hordeaceus subsp. hordeaceus 97/95

Bromus japonicus 9/36 Bromus tectorum 75/91 Buddleja davidii 0/41

Camelina microcarpa subsp. sylvestris 9/41

Cannabis ruderalis 13/41 Cardaria draba 59/86 Chenopodium ambrosioides 0/23

Chenopodium botrys 6/50

Chenopodium strictum 91/95

Consolida regalis 28/59

Conyza canadensis 100/100

Crepis foetida subsp. rhoeadifolia 13/50

Cuscuta campestris 9/36 Cynodon dactylon 22/77

Daucus carota subsp. carota 81/100

Descurainia sophia 84/86 Diplotaxis muralis 9/36 Diplotaxis tenuifolia 34/77

Echinochloa crus-galli 91/91

Echium vulgare 94/95 Eragrostis minor 44/100 Erigeron annuus 66/100 Erodium cicutarium 50/91

Erucastrum gallicum 0/36 Fraxinus pennsylvanica 6/32

Galeopsis angustifolia 0/23 Geranium pussilum 50/95 Geranium pyrenaicum 16/41

Juglans regia 22/55

Lamium amplexicaule 22/64
Lamium purpureum 66/91
Lathyrus tuberosus 38/82
Lepidium campestre 22/50
Lepidium densiflorum 34/59

Lepidium virginicum 16/45 Lithospermum arvense 9/36

Medicago lupulina 91/100

Medicago sativa 56/86 Melilotus officinalis 84/86

Microrrhinum minus 44/73

Morus alba 0/41

Onobrychis viciifolia 3/64 Oxalis corniculata 3/23 Papaver rhoeas 81/91 Parietaria officinalis 0/27

Pastinaca sativa subsp. sativa 38/82

Petrorhagia prolifera 25/59

Populus alba 13/64

Populus cf. × canadensis 78/86

Portulaca oleracea 22/55

Reseda lutea 69/91 Rumex patientia 13/50

Setaria pumila 44/73 Setaria verticillata 31/68

Setaria viridis subsp. viridis 72/91 Sisymbrium orientale s.l. 22/55

Solidago gigantea 25/82 Stachys annua 3/41 Torilis arvensis 0/23

Tragopogon dubius 41/73 Verbena officinalis 3/86 Veronica arvensis 59/95 Veronica persica 50/82

Vicia angustifolia agg. 41/100

Vicia villosa 25/50 Vulpia myuros 28/64

Xanthium saccharatum 0/32

The species (taxa) showing no significantly different distribution between the individual waterways:

Abutilon theophrasti

Acer negundo Acorus calamus

Aesculus hippocastanum Ailanthus altissima Alopecurus myosuroides Amaranthus blitum Amaranthus hybridus Amaranthus × ozanonii Amaranthus retroflexus

Anchusa officinalis
Anethum graveolens
Anthemis arvensis
Antirrhinum majus
Apera spica-venti
Arctium minus
Armoracia rusticana

Armoracia rusiicana Arrhenatherum elatius Artemisia absinthium

Artemisia annua

Asperugo procumbens

Aster simplex Atriplex patula Avena fatua Avena sativa

Ballota nigra subsp. nigra

Bellis perennis Berteroa incana

Brassica napus subsp. napus

Brassica nigra Bromus inermis Bromus sterilis Bryonia alba

Bryonia dioica

Bunias orientalis Calendula officinalis

Capsella bursa-pastoris Carduus acanthoides

Centaurea cyanus

Chenopodium ficifolium
Chenopodium glaucum
Chenopodium hybridum
Chenopodium missouriense
Chenopodium murale

Chenopodium polyspermum Chenopodium probstii

Cichorium intybus subsp. intybus

Cirsium arvense Cirsium vulgare

Commelina communis
Conium maculatum
Consolida orientalis

Convolvulus arvensis

Cornus sericea
Crepis biennis
Crepis capillaris
Crepis tectorum
Cymbalaria muralis
Datura stramonium
Digitaria ischaemum

Digitaria sanguinalis subsp. pectiniformis Digitaria sanguinalis subsp. sanguinalis Dipsacus fullonum

Echinops sphaerocephalus

Epilobium ciliatum
Eryngium campestre
Euphorbia helioscopia
Euphorbia peplus
Fagopyrum tataricum

Geranium dissectum Helianthus ×laetiflorus

Helianthus annuus var. macrocarpus

Helianthus tuberosus Hibiscus trionum Hordeum distichon Hordeum murinum

Hordeum vulgare subsp. vulgare

Impatiens parviflora Isatis tinctoria

Kochia scoparia subsp. densiflora Kochia scoparia subsp. scoparia

Lactuca serriola
Lapsana communis
Lathyrus latifolius
Lepidium ruderale
Leucosinapis alba
Linaria vulgaris
Lolium multiflorum
Lycium barbarum
Malus domestica
Malva neglecta
Malva sylvestris
Matricaria discoidea

Matricaria discoidea
Matricaria recutita
Medicago × varia
Melilotus albus

Mentha × rotundifolia

Mentha arvensis
Mercurialis annua
Myosotis arvensis
Myosotis stricta
Oenothera depressa
Oenothera glazioviana
Oenothera pycnocarpa
Onopordum acanthium

Oxalis dillenii

Oxalis fontana Silene latifolia subsp. alba

Panicum capillare subsp. capillare Silene noctiflora

Papaver argemoneSinapis arvensisParthenocissus insertaSisymbrium altissimumPhacelia tanacetifoliaSisymbrium volgense

Phalaris canariensisSolanum decipiensPisum sativum subsp. sativumSolanum lycopersicumPlantago major subsp. majorSolanum nigrum s.s.

Polygonum arenastrum
Solidago canadensis
Potentilla intermedia
Sonchus arvensis
Prunus cerasus
Sonchus asper

Prunus domesticaSonchus oleraceusPyrus communisSorghum halepenseRaphanus raphanistrumSyringa vulgaris

Raphanus sativus Tilia × euchlora Reseda luteola Torilis japonica Reynoutria japonica vax. japonica Trifolium hybridum

Robinia pseudacacia Triticum aestivum

Rubus armeniacus Urtica urens

Salvia verticillata Verbascum densiflorum

Saponaria officinalis

Secale cereale

Vicia hirsuta

Sedum rupestre subsp. erectum

Vicia tetrasperma

Sedum spurium Viola arvensis
Senecio inaequidens Viola odorata

Senecio vernalis Xanthium strumarium

Senecio vulgaris

# Appendix 2

**Table 3.** Summary of the port localities areas and years of investigation of 54 Central European river ports used in the study.

| River port (country)                                    | Port locality area [m <sup>2</sup> ] | Years of investigation   |
|---|--------------------------------------|--------------------------|
| Elbe and Vltava Rivers                                  |                                      |                          |
| 1. Hamburg (Germany)                                    | 74 400 000                           | 1980, 88, 91, 95         |
| 2.Wittenberge (Germany)                                 | 5 143                                | 1979, 85, 87, 97         |
| 3. Tangermünde (Germany)                                | 36 423                               | 1987, 97                 |
| 4. Magdeburg-Rothensee (Germany)                        | 906 672                              | 1997, 98                 |
| 5. Magdebur, Industriehafen (Germany)                   | 2 017 555                            | 1980, 85, 87, 97, 98     |
| 6.Magdeburg, Handelshafen (Germany)                     | 268 722                              | 1979, 80, 85, 87, 97, 98 |
| 7. Schönebeck-Frohse                                    | 128 203                              | 1979, 80, 85, 87, 97, 98 |
| 8. Aken, Handelshafen (Germany)                         | 93 547                               | 1987, 97                 |
| 9. Torgau (Germany)                                     | 100 048                              | 1979, 87, 97             |
| 10. Riesa-Gröba, Industriehafen (Germany)               | 2 194 650                            | 1979, 80, 87, 97, 98     |
| 11. Riesa, transshipment point at mill houses (Germany) | 15 398                               | 1979, 80, 87, 91, 97     |
| 12.Dresden, Albertshafen (Germany)                      | 337 191                              | 1979, 87, 91, 97         |

| River port (country)  | Port locality area [m²] | Years of investigation   |
|---|-------------------------|--|
| 13.Děčín-Loubí (Czech Republic)                                 | 51 630                  | 1968, 74, 75, 78, 79, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 95, 96, 97, 98, 99, 2000, 03, 04, 05, 06, 07         |
| 14. Děčín-Staré Loubí (Czech Republic)                          | 20 241                  | 1968, 74, 87, 93, 95, 96, 97, 98, 99, 2000, 04, 05   |
| 15. Děčín-Staré Město (Czech Republic)                          | 3 524                   | 2000   |
| 16. Děčín-Rozbělesy (Czech Republic)                            | 553 337                 | 1974, 87, 90, 91, 92, 95, 2005, 07, 08, 09   |
| 17. Ústí nad Labem-Krásné Březno (Czech Republic)               | 17 285                  | 1968, 74, 75, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 95, 96, 97, 98, 99, 2000, 04                     |
| 18. Ústí nad Labem, Central Port (Czech Republic)               | 151 096                 | 1990, 91, 92, 93, 94, 95, 96, 97, 98, 99, 2000, 04, 05   |
| 19. Ústí nad Labem, Western Port (Czech Republic)               | 113 993                 | 1968, 74, 75, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 99, 2000, 03, 04, 05, 06, 07     |
| 20. Ústí nad Labem, Větruše (Czech Republic)                    | 27 885                  | 1968, 73, 74, 75, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 95, 97, 2000   |
| 21. Ústí nad Labem-Vaňov (Czech Republic)                       | 37 598                  | 1974, 75, 89, 92, 93, 95, 97, 2000, 04   |
| 22. Lovosice, Canal Port (Czech Republic)                       | 49 346                  | 1968, 69, 72, 74, 75, 76, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 95, 96, 97, 2000, 04, 05, 07             |
| 23.Lovosice-Prosmyky (Czech Republic)                           | 772 847                 | 1996, 97, 2000, 09   |
| 24. Mělník-Pšovka (Czech Republic)                              | 118 689                 | 1968, 69, 71, 72, 74, 75, 76, 78, 79, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 95, 99, 2000, 04, 05, 06, 08, 09     |
| 25. Mělník, Transshipment Point (Czech Republic)                | 56 487                  | 1972, 73, 74, 75, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 95, 99, 2000, 09                             |
| 26. Kolín, Transshipment Point (Czech Republic)                 | 12 584                  | 1987, 91, 92, 93, 95, 96, 97, 2000, 04   |
| 27. Týnec nad Labem, Ro-Ro-Transshipment Point (Czech Republic) | 5 585                   | 1992, 95, 97, 2000   |
| 28. Chvaletice (Czech Republic)                                 | 19 376                  | 1987, 88, 91, 92, 95, 2000   |
| 29. Miřejovice Ro-Ro-Transshipment Point (Czech Republic)       | 31 313                  | 1992, 95, 97, 2000   |
| 30. Praha-Holešovice (Czech Republic)                           | 122 402                 | 1968, 69, 70, 71, 72, 73, 74, 75, 76, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 98, 99, 2001, 06 |
| 31. Praha-Smíchov (Czech Republic)                              | 20 044                  | 1996, 97, 99, 2000, 05, 06, 08, 09   |
| 32. Praha-Radotín (Czech Republic)                              | 16 727                  | 1992, 93, 94, 96, 99, 2006   |
| Danube river  |                         |  |
| 34. Baja (Hungary)  | 362 773                 | 1982, 89, 94   |
| 35. Dunaújváros (Hungary)                                       | 60 591                  | 1994   |
| 36. Budapest-Csepel (Hungary)                                   | 2 640 118               | 1982, 89, 94   |
| 37. Budapest-Ferencváros (Hungary)                              | 3 013 144               | 1982, 89, 94   |
| 38. Györ, Transshipment Point (Hungary)                         | 960 530                 | 1982, 89, 94   |
| 39. Györ, Commercial Port "Iparcsatorna" (Hungary)              | 140 892                 | 1989, 94   |
| 40. Komárno (Slovakia)  | 210 567                 | 1968, 73, 76, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 98, 99, 2000, 03, 04, 05                                 |
| 41. Bratislava-Pálenisko (Slovakia)                             | 842 843                 | 1986, 87, 88, 90, 91, 92, 98, 2003, 04, 05, 08   |
| 42. Bratislava-Nivy (Slovakia)                                  | 415 605                 | 1968, 73, 74, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 98, 2003, 05, 08   |
| 43. Wien-Lobau (Austria)  | 1 915 257               | 1990, 92, 93, 98   |
| 44. Wien-Albern (Austria)                                       | 119 731                 | 1990, 92, 93, 98   |
| 45. Wien-Freudenau (Austria)                                    | 862 591                 | 1990, 92, 93, 98   |
| 46. Krems an der Donau (Austria)                                | 529 067                 | 1990, 92, 93, 98   |
| 47. Ennsdorf, Hafenbecken Ost, Silos (Austria)                  | 152 737                 | 1997, 98   |
| 48. Enns (Austria)  | 711 666                 | 1997, 98   |
| 49. Linz, Tankhafen (Austria)                                   | 1 636 055               | 1990, 92, 93, 94, 97   |
| 50. Linz, Handelshafen /Stadthafen (Austria)                    | 1 375 666               | 1900, 92, 93, 94, 97   |
| 51. Passau-Racklau (Germany)                                    | 36 308                  | 1989, 97   |
| 52. Deggendorf (Germany)  | 408 775                 | 1989, 97   |
| 53. Regensburg, Osthafen (Germany)                              | 435 161                 | 1989, 91, 97   |
| 54. Regensburg Westhafen/Luitpoldhafen (Germany)                | 724 553                 | 1989, 91, 97   |

## Supplementary material I

#### Electronic data set

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Data type: species data

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